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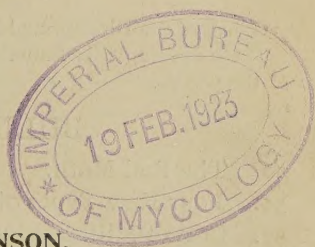
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Edema of the Tomato.



By GEO. F. ATKINSON.

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CEDEMA OF THE TOMATO.

During the latter part of October, 1892, tomato plants, of a variety No. 18, grown in the forcing houses of the Horticultural Department, presented a very peculiar appearance. The plants were at some little distance from the main passage way in the tomato house through which I occasionally passed. For this reason, and also because no complaint was entered by the growers, the trouble escaped my notice. The plants presented to me the appearance of having been recently transplanted, many of the compound leaves having a curved pendent position, though the leaflets were usually curved strongly upward, showing the lighter color of the under surface. It was suggested at that time that this peculiar position of the leaf and curl of the leaflets was a peculiarity of the variety. Upon each of several following visits to the forcing house, at intervals of four to six days, the peculiar appearance of these plants fastened my attention for a few minutes. Upon one visit I had occasion to pass the bench upon which they were growing, and could not resist the impulse to look more closely at the character of the curled leaf.

It was at once apparent that this peculiar appearance was not normal to the plant. The veinlets as well as the midrib, petioles, and the surface of the stem presented numerous elevated areas of a frosty aspect as shown in figures 1 and 2, in Plate I. Their resemblance to masses of conidia formed in the early stages of some of the *Erysipheæ* was very striking. Examined with a pocket lens a mass of minute rounded bodies could be seen which still bore some resemblance to conidia of the powdery mildews. The rounded particles possessed a gleaming aspect and did not lie so loosely nor appear in chains as is the case with these mildews. A little further observation showed that great injury to the plant followed in the latter phases of the trouble.

It was quite natural before recourse to a microscopic examination to attribute the mildewed aspect of the leaves and the dying of the leaves in the later stages to the operation of some fungus. But a section through one of these areas revealed under the

microscope a very different state of things. The affected areas had the appearance of a cushion similar to an erinoid or hypertrophied condition of the tissue. The epidermal cells were very much enlarged while the chlorophyll bearing cells just beneath as well as some of the more deeply seated cells were greatly elongated in a radial direction, and strongly clavate at their outer extremity where this extended beyond the lateral pressure from adjacent tissue. In many cases the epidermal cells quickly separate and slough off. The cells of the affected areas possessed exceedingly delicate walls so that with little disturbance they would collapse. There was little protoplasm in proportion to the size of the cell and a corresponding amount of cell sap.

Several of the notable phenomena coincident with the development of these cushions of abnormally turgescient tissue are explained by this peculiar physical derangement of the normal cell structure. The frosted or whitened aspect of the cushions results from the small amount of chlorophyll in proportion to the leaf surface. The amount of chlorophyll in the individual cell remains the same while the grains are far separated in their distribution throughout the greatly enlarged cell. The curling upward of the leaves results from the greater lateral pressure which exists in the cells of the lower surface of the veins.

A comparison of the normal tissue with that of the cushions will serve to show the profound changes accompanying their development. From serial sections made through several of these cushions on the leaf veins two sections were selected from one series to illustrate the changes in this part of the leaf. Camera lucida drawings were made from these two sections magnified to the same scale. One of these represented in figure 4 was taken from the leaf vein just before the series of sections entered the cushion and practically represents the normal arrangement and form of the cells of the leaf vein. Figure 5 represents one of the serial sections of the same leaf vein, the section having been taken from the center of the cushion. Each end of the section at *a* represents relatively the normal condition of the cells of the leaf. The line of epidermal cells, *e, e*, is still adhering for some distance, but at the summit of the cushion they have fallen away. A comparison with the normal epidermal cells shows how much they have been enlarged. The sub epidermal cells have undergone

the most profound change, being eight to ten times their normal size. Some of the deeper lying cells have also elongated radially, while others have become abnormally enlarged. It will be observed that the distention of the cells has not only profoundly changed their normal form, but the crowding one upon another has displaced many others. A study of the series of sections from such a cushion, as well as the study of one in an early stage of development, shows that the epidermal cells nearly always first partake of the radial elongation. These are followed by the sub-epidermal layer and so on.

Serial sections through the cushions on the stem were also made. Three from a series through quite a young cushion on the stem are reproduced by camera lucida drawings in figures 9, 10 and 11.

Figure 9 represents a section taken from the edge of the cushion and shows the early stage in the elongation of a few epidermal cells. In this section is also shown a peculiarity in the early elongation of some of the more deeply seated cells. A few of the cells of the collenchyma have elongated radially before those lying immediately outside of them have changed their form. This rarely occurs, and by the time the sections approach the center of the cushion the successional changes of the layers of cells from the outside exists in the usual manner. It is to be noted in connection with the elongation of the cells of the collenchyma, that while such thick-angled tissue offers support to the stem, little more resistance is offered to the radial elongation of the cells by this tissue than by parenchyma. The lateral walls being thin permit the cell membrane to be stretched. Figure 11 is one of the series from the center of this very young cushion. Figure 12 is from an older cushion on a much older part of the stem of the same variety. Here many of the epidermal cells have sloughed off and others are nearly free. The hypodermal layer, chlorophyll bearing layer, is remarkably elongated, while the first layer of the collenchyma is also changed. In the older cushions the radial elongation effects also deeper layers of the collenchyma, sometimes two or three layers. Usually by the time such changes occur to any marked degree in the deeper layers, the sub-epidermal portion of the cushion is in a state of collapse. This effect is partially shown in figures 13 and 15.

On the leaves of some plants there frequently is very little evidence to the unaided eye of the presence of these cushions. But here and there, upon close examination, can be seen very minute elevations. Magnified with a pocket lens they present the appearance shown in figure 6. They appear to be located entirely in the mesophyll of the leaf, or more properly speaking, at or near the terminations of some of the veinlets. This probably accounts for their small size. Being located in such delicate tissue they rapidly collapse and disappear from view.

Figures 7 and 8 represent sections selected from serial sections through one of these small mesophyll cushions. Figure 7 is taken from the edge and shows the remarkable enlargement of two of the epidermal cells. Near by can be seen the termination of a vascular bundle. Figure 8 is from the center of the same mesophyll cushion. Passing from each end of the section toward the center an idea can be formed of the progressive elongation of the different cell layers. The tissues at the summit of the cushion are in a state of collapse. This one is remarkable from the fact that the elongation has advanced from the epidermal layer of the under side of the leaf through the parenchyma until the palisade cells of the upper side of the leaf are concerned, and their elongation is in the same direction, *i. e.*, toward the lower side of the leaf. This results from the fact that the progressive elongation, beginning at the lower side of the leaf and advancing toward the upper, has relieved the pressure from adjacent cells on the lower side, and also that the primary enlargement of the cells of the under side caused the leaf, at this point, to arch downward, which in itself would make the lower side of the cells the point of the least resistance. Figures 6, 7 and 8 are from plants sent by L. R. Jones, Horticulturist of the Vermont Station. Very rarely, I have noted in a few instances in the forcing house, cushions are formed upon the upper side of the leaf.

The primary effects of this derangement of the tissue, farther than is pointed out above, relates to certain interferences with the life and nutrition of the plant which are manifestly attributable to it. When the cell walls have become so inordinately stretched that they suddenly collapse, as frequently happens, the changes brought about by the escape of water from this and adjacent tissues during the warmer part of the day may be so profound as

to cause the leaf to wilt and die. In other cases, the cushions when collapsed soon dry without great loss of water from adjacent tissues, but the injury is so deep it seriously disturbs the nutrition of that part of the leaf as shown by a yellowing of the upper surface at this point. Numerous points of attack on the venation of the lower surface of the leaf in such cases gives to the upper surface a spotted appearance, while the dried cushion immediately below presents a tomentose appearance. Although in such cases the entire leaf is usually curled upward, the points of injury are more strongly arched, which produces upon the upper surface of the leaf a depressed area within the yellow spots.

The secondary effects of the trouble relate to profound changes which sometimes follow, but which are not so manifestly attributable in all cases, at first examination, to this derangement of the tissues. Frequently, when the leaf does not wilt after the collapse of the cushion, the broken and dying tissues encourage the development of putrefactive germs which set up fermentations that affect adjoining tissues and the leaf is slowly disorganized. Discoloration of the tissue accompanies these morbid phenomena, and while they proceed also through the very succulent parenchymatous tissue of the petiole and down the stem, there appear elongated, depressed, blackened areas, which eventually reach the vascular tissue of the stem.

Frequently such morbid changes originate from cushions developed on the stem, and there is reason to believe that sometimes quite extensive areas of hypodermal tissue of the stem are stretched enormously and induce similar destructive metabolism when the epidermis has become too firm for its individual cells to participate in such change.

When the development of the cushions is confined mainly to the mesophyll areas of the leaf, or to the very small veinlets, or at their terminations, they rapidly collapse and the morbid changes succeeding in the mesophyll extend over areas of various sizes, which in the early stages are yellowish in color. In these secondary effects many of the very small young leaves are affected at the apex, frequently the entire apex being involved, and on the somewhat larger leaves it may be confined chiefly to the base of the leaf, or the severity of the attack is located there. The progress of this yellow color indicates failing nutrition which is

augmented by the interference produced from the diseased areas in the stem. It terminates in the death of the tissues involved, which then change to a dirty greyish brown color. The veinlets involved become much darker in color, being nearly black, so that viewed through a pocket lens the greyish brown patches show frequently cross lines of black or borders of the same color.

Inquiry into the governing cause. Having observed the external aspect and progress of development of these cushions, as well as their minute anatomy and relation to the well being of the plant, the inquiry into their cause presents itself. The existence of any fungus of ordinary dimensions standing in causal relation was easily disposed of. Their superficial resemblance to the erineum developed on the leaves of various species of birch, maple, alder, etc., through the stimulus induced by irritation from phytoptid mites, suggested a similar symbiont upon the tomato plant. But careful examination proved this suspicion to be groundless.

By this process of elimination of suspected causes, the enquiry was gradually removed from the region of the possible symbiosis of some one of the more prominent and easily recognizable microscopic forms to that of the possible relation of some form of bacteria which, by its presence within or upon the affected organs, excited them to this abnormal development.

Two lines of investigation were carried out, having in view the discovery of the causal germ. One of these proceeded upon the more customary, but less scientific, lines of enquiry usually adopted in the study of the bacteria of plant diseases, viz.: the inoculation with diseased material; the other proceeded upon the more rational line of enquiry chiefly adopted in the study of the bacteria of animal diseases, viz.: the separation of the germs present and inoculations with pure cultures to determine the specific germ.

Inoculations of healthy plants with diseased material. *Experiment No. 1*, December 3, 1892. Macerated tissue from freshly developed cushions was gently rubbed between the thumb and finger upon the leaves and stem of a healthy plant. Portions

of the affected plant were also left pendent upon the healthy one. *No result.*

Experiment No. 2, December 3, 1892. Macerated tissue from a plant in the later stages of disorganization was gently rubbed between the thumb and finger upon the leaves and stem of a healthy plant. A portion also of the diseased plant was left pendent upon the healthy one. *No result.*

Experiment No. 3, December 3, 1892. Twenty very young plants freshly potted, just developing the plumule, were treated as follows: There were four rows, five plants in each row. To one plant in each row was applied some of the macerated tissue from freshly developed cushions. Likewise to one plant in each row was applied some of the macerated tissue from a plant in the later stage of the disease. *No result.*

Experiment No. 4, December 3, 1892. In a potted plant were made several slit wounds with a scalpel, parallel with the axis of the stem and petiole. Into these were introduced thin longitudinal slices of tissue from freshly developed cushions. The wounds were then wrapped with fresh tomato leaves and tied loosely to prevent too great evaporation from the wound. The plant was thoroughly sprayed with water also. *No result.*

Experiment No. 5, December 3, 1892. In like manner a potted plant was inoculated with longitudinal slices from a stem in the later stages of the disease. *No result.*

Separation of bacteria from affected plants. By the use of sterilized instruments and with precautions against contamination from the outside, portions of the interior of freshly developed cushions were transferred to nutrient agar which contained an infusion of tomato plant. *No growth appeared.*

Portions of the cushions including the external parts were then macerated in sterilized distilled water, and the dilution was farther diluted in the usual way in three tubes of liquid nutrient agar containing tomato plant infusion. Esmarch rolls and cultures in Petrie dishes were made of these, and several different bacteria were isolated.

In like manner leaves of plants in the later stages of the disease were macerated and carried through dilutions to isolate bacteria. Also tissue from the internal parts of petioles and stems in the later stages of the disease were used for dilution cultures.

From several such dilution cultures there were obtained fifteen different species of bacteria which were grown in pure cultures and used for inoculations. Of these there were three species of *Bacillus*, three of *Micrococcus* and the remainder probably species of *Bacterium*. One *Micrococcus* and four species of *Bacterium* were chromogenous forms. The chromogenous forms and one species of *Bacillus* (*B. figurans*) were not considered suspicious, but it was very little additional trouble to carry on cultures of these.

When the organisms were isolated they were grown in quantity in a liquid culture consisting of equal parts of bouillon and tomato plant infusion.

Experiment No. 6, December 19, 1892. Inoculations were made with liquid cultures of the bacteria as follows: The liquid containing the cultures was gently rubbed between the thumb and finger upon the surface of the stem and leaves. Also with a needle abrasions were made of the surface tissue of petioles and stems introducing in this manner into the superficial tissues some of the organisms. *No result.*

The entire series of inoculations was made in such a way that several duplicate inoculations were made of all the germs present which could possibly bear any relation to the trouble. The negative results point to the possibility that there is some disturbance of the equilibrium of the natural forces and physiological processes in the plant. This suspicion is strengthened by the fact that the cushion is not formed by ordinary hypertrophy which is accompanied by increase of nutriment at that point, and multiplication of cells. Ordinarily, there is no increase in the number of the cells. When this does occur it takes place in the deeply seated cells which do not suffer collapse while the more superficial ones break down. The increase in the number of cells in such cases occurs simply by the formation of transverse walls in the elongated cells.

Is the trouble a physiological one? The abnormal stretching of groups of cells to eight to ten times their normal size would then be sought for in the excessive activity of one or more of the physiological processes which contribute to turgescence and in the lesser activity of those processes which relieve it.

The most important of these seems to be the excess of root

pressure over transpiration. It will be instructive to consider the conditions of environment which have united to disturb the desirable stability of equilibrium of these two forces in the plant.

The close confinement of the plants in the forcing house where there is little agitation of the air, must necessarily lessen the rapidity and amount of transpiration compared with what would take place in the open. The water vapor freed through transpiration from plants grown in the open under natural conditions is quickly carried away by currents of air* which are to a greater or less extent in almost constant action. This permits then a more active transpiration than could take place should the water vapor remain undisturbed near the foliar organs. Even should the water vapor escape from the neighborhood of the transpiring surfaces only through the law of diffusion plants in the open would be at a greater advantage than those grown in the confined quarters of the forcing house. That transpiration is obstructed by the humidity of the atmosphere has been abundantly shown.†

* Sachs Physiology, p. 554.

Höhnel, Ueber den Gang d. Wassergehaltes und Transpiration bei Entwicklung d. Blattes, 1878. Cited by Pfeffer, p. 144.

Wiesner, Grundversuche ueber den Einfluss der Luftbewegung auf die Transpiration. Bot. Centralb., viii, pp. 382-383.

Wind according to Wiesner in most cases accelerates transpiration. In some cases (*Saxifraga sarmentosa*) it closes the stomates and therefore retards transpiration. See same title in P. A. Wien, Abth. i, Bd. xcvi, pp. 182-214. Cited in Just's Bot. Jahrbücher, 1888, 1, pp. 83-84.

† Unger, Sitzungsbericht d. Wiener Akademie, Bd. xliiv, 2, 1861.

Sachs, Handbuch der Experimental-Physiologie, 1865. Sitzungsab. d. Wien. Akad. Bd. xxvi.

Déherain, Comptes Rendus, T, lxi.

Masure, Untersuchungen über die Verdunstung des freien Wassers, des im Ackerbodenenthaltene Wasser, und über die transpiration der Pflanzen, Ann. Agronomiques, T, vi, fasc. iii, pp. 441-500.

Reinitzer, Ueber die physiologische Bedeutung der Transpiration der Pflanzen. Sitzungsberichte der K. K. Acad. d. Wissenschaft, 1881, 1, Abth.

LeClerc, De la transpiration dans les végétaux, Ann. d. Sc. Nat. T, xvi, 1883, pp. 231-279.

Tschaplowitz, Giebt es ein Transpiration-Optimum? Beitrag zur Theorie der Vegetationsconstanten Bot. Zeit., Jahrg. 41, No. 22, S. 353-362.

Kohl, Die Transpiration der Pflanzen, etc., Braunschweig, 1886.

Eberdt, Die Transpiration d. Pflanzen und ihre Abhängigkeit von äusseren Bedingungen, Marburg, 1889.

Goodale, Physiological Botany.

Transpiration is less active during the night than in the day, not only because of the lower temperature of the air, but especially because of the absence of light.* During the winter season when plants are grown in the forcing houses the nights are much longer than the days and the total amount of transpiration in 24 hours, other things being equal, would be less than what would take place in the open during the summer months when the days are much longer than the nights. Add to this the marked number of cloudy days during the winter, with a low sun offering at best but a feeble light, and the conditions for transpiration are still more unfavorable.

Still another factor must be considered which deprives the plants of much light, the structure of the forcing house itself. The light is not so intense when it passes through glass, though the amount of light thus cut off may be very little. However, the frame work, walls and partitions do cut off an appreciable amount of light.

These considerations, showing a lessened amount of transpiration compared with what takes place under natural conditions when the plants are grown out doors, would place root pressure in excess of transpiration should the conditions for root pressure under both circumstances be the same.

With the comparatively small amount of light carbon assimilation is lessened, so that the plant under the forced conditions of growth, when it needs larger quantities of carbohydrates has to do with really a less quantity than is supplied in the open where conditions for rapid growth are not so favorable and those for assimilation are improved.

*Sach's Physiology.

Goodale, Physiological Botany.

Unger, Sitzungsab., Wien. Akad., Bd. xlv, 2, 1861.

Déherain, Compt. Rend. Paris. T. lxi.

Masure, Ann. Agronomique, T. vi, fasc. pp. 441-500.

Reinitzer, Sitzungsab., d. K. K. Acad. Wiss., 1881, I.

Leclerc, Ann. Sci. Nat. Bot. T. xvi, 1883, pp. 231-279.

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Burgenstein, Material zu einer Monographie der Transpiration, Verhandlungen d. K. K. Zool. Bot. Gesellsch., Zu Wien Vol. 37, 1887, pp. 691-782, and Vol. 39, 1889.

Soil temperature compared with that of the air. Some observations made upon the temperature of the soil and air in the tomato house indicate that the soil is maintained at a temperature only a few degrees below that of the air. A sufficient number of observations have not been made to show what bearing the difference in temperature between the two media has upon the relation of root pressure to transpiration. At the lower benches (those at the side of the house where the glass is quite close to the beds) the soil, from a few observations, possessed a temperature of 2° to 5° Fahr. lower than the air, while in the center of the house,

TABLE OF COMPARATIVE SOIL AND AIR TEMPERATURES,
(FAHRENHEIT.)

		7 A. M.	1 P. M.	7 P. M.	MEAN.
May, 1891	Inches.				
	Air.....	47.04	61.75	53.30	54.04
	1 Soil.....	46.54	54.03	52.93	51.17
	3 Soil.....	54.31	53.73	52.87	53.63
	6 Soil.....	47.49	49.27	51.24	49.33
	9 Soil.....	47.83	48.22	49.36	48.80
	12 Soil.....	47.64	47.63	47.90	47.72
	24 Soil.....	45.00	45.14	45.20	45.10
	36 Soil.....	43.78	43.49	43.50	43.59
	Mean of Soil.....	45.47	46.40	46.45	46.10
June, 1891	Air.....	58.28	72.42	65.38	65.36
	1 Soil.....	59.18	65.42	64.53	63.04
	3 Soil.....	59.10	64.80	64.21	62.70
	6 Soil.....	59.43	60.40	61.73	60.52
	9 Soil.....	59.23	58.96	59.67	59.28
	12 Soil.....	58.79	58.37	58.60	58.58
	24 Soil.....	54.00	54.12	54.11	54.07
	36 Soil.....	51.25	51.35	51.37	51.32
	Mean of Soil.....	54.80	55.68	55.74	55.40
July, 1891	Air.....	64.08	76.05	68.81	69.65
	1 Soil.....	62.70	68.59	67.44	66.24
	3 Soil.....	62.78	67.56	67.10	65.81
	6 Soil.....	63.08	64.23	65.18	64.16
	9 Soil.....	63.17	63.18	62.85	63.07
	12 Soil.....	62.39	62.14	62.44	62.32
	24 Soil.....	58.16	58.25	58.26	58.22
	36 Soil.....	55.75	55.82	55.82	55.79
	Mean of Soil.....	58.91	59.73	59.69	59.44

where there was an opportunity for the warm air to rise toward the ridge, the difference in soil and air temperature was greater, being more marked the higher the elevation at which the temperature was taken in the air.

In the absence of careful data covering a period of several weeks there could not be made any satisfactory comparison with the difference between soil and air temperature out doors during the growing months. However, it will be interesting to note such differences in this connection. For this reason there is appended here a table of soil and air temperatures adapted from data published by President Fernald of the Maine Agr. Exp. Station.*

The difference in the mean temperature of the soil (from 1-36 inches) and air for May, June and July is thus seen to be approximately 10° Fahr. Comparing the temperature of the soil from 1-12 inches it is found to be from 5°-6° Fahr. below the mean temperature of the air. It is doubtful, however, if these temperatures taken only at the stated times of day really give the information desired in relation to the bearing of soil and air temperatures on root pressure and transpiration. For through the day when the temperature is the highest that of the air is still higher and with the aid of light and agitation of the air transpiration is sufficient to relieve the plant. The early period of the night is the time when out doors the conditions for root pressure as indicated by temperature would be more favorable than they would for transpiration. But terrestrial radiation soon lowers the temperature of the soil so that the plants exist under this disadvantage a comparatively short time.

Here again it is necessary to bear in mind the very short nights during which transpiration is low in comparison with the long days when it is very active. The light conditions are reversed in the forcing house and frequently the light is very feeble with little agitation of the air while there is a continued maintenance of soil temperatures suitable for active root absorption. Thus while it cannot be asserted positively that the temperatures of the forcing house are such as to add to the complex disturbance of

*Annual Report, Part IV, Maine State College Agr. Exp. Station, pp. 155-174.

the physiological processes, there are indications that such is the case.

Since turgescence is mainly dependent upon root absorption for the supply of water and a turgid condition of the plant soon follows strong root pressure unless transpiration is taking place rapidly, it has become customary to say that root pressure causes turgidity. Of course, it is understood that this is not the immediate cause. Water cannot be pressed into a cell and cause turgescence. The cell wall is permeable and as rapidly as water could be driven in at one side it would filter out at the other. The protoplasmic utricle* which lines the cell wall is not permeable, or at least only to a small degree. The water, then, which passes into the cell through the protoplasmic utricle, cannot filter out, and when it does not escape by evaporation or exosmose from the surface, it stretches the protoplasmic utricle, presses it against the elastic cell wall which then yields and the cell is turgid. The extent to which the cell wall is stretched depends upon the endosmotic activity which introduces water into the cell, the rate of transpiration and the firmness of the cell wall. The endosmotic activity within the cell is brought about by the presence of certain salts or organic acids in the cell sap which have a strong affinity for water.†

By root absorption the plant is supplied with water, the permeable cell wall permitting it to flow from the vascular bundles into the fundamental and other tissues where it comes in contact

*Mohl. Bot. Zeitung, 1846, p. 75.

Nægeli, Pflanzenphysiologische Untersuch. Heft I, 1855, p. 1.

Pfeffer, Osmotische Untersuchungen. Leipzig 1877.

Sachs' Physiology.

Goodale, Physiological Botany.

†De Vries, Ueber die Ausdehnung wachsender Pflanzenzellen durch ihren Turgor, Vorläufige Mittheilung; Bot. Zeit. 1877, S., 1-10.

Untersuchungen über die mechanischen Ursachen der Zellstreckung von der Einwirkung von Salzlösungen auf den Turgor wachsenden Pflanzenzellen, Leipzig, 1877. See Justs Bot. Jahresb. 1877, I, p. 65-67.

Ueber die Bedeutung der Pflanzensäuren für den Turgor der Zellen. Bot. Zeit. 1879, p. 847.

Palladin, Athmung und Wachsthum, Berichte d. Deutsch. Bot. Gesellschaft, 1886, pp. 322-328.

‡ Bildung der organischer Säuren in den wachsenden Pflanzentheilen, Ber. d. Deuts. Bot. Gesellschaft, 1887, p. 325.

with the protoplasmic membrane lining the cell wall. When root absorption is active and transpiration is inactive or at a low ebb, the affinity which the vegetable acids possess for the water draws it within the cells. Root absorption practically being in operation continuously under the conditions of the forcing house, and transpiration being in operation for such a large part of the time, the cell walls are unduly stretched. This continues until a point is reached where the normal tissue tension is overcome and the fundamental tissue of the leaf or the cortical parenchyma of the stem is no longer held in longitudinal tension. The cell wall thus continuing to stretch yields at the point of least resistance which is at the surface of the congested tissue and the radial elongation of the cells is the result.

The organic acids increase most rapidly at a temperature ranging from 50° to 57° Fahr.* As the temperature rises above this point they are gradually decomposed. Darkness or weak light also favors their increase and De Vries† has shown that a periodicity of increase or decrease of these acids exists corresponding to night and day. In fact anything which interferes with oxidation serves to permit their increase while those conditions which promote oxidation serve to decrease them.‡ According to Warburg it is not the direct action of light which decomposes these organic acids but the oxygen set free during carbon assimilation.||

Another effect of the feeble light and its short duration is the proportionately small quantity of carbohydrates produced. Except in the case of some shade plants where direct solar light may be too intense for normal assimilation, other things being

*De Vries, Ueber den Antheil der Pflanzensäuren an die Turgorkraft wachsender Organe. Bot. Zeit. 1883, S. 850.

Warburg, Untersuchungen aus d. Bot. Inst. 2. Tübingen, Vol. 2. Heft I, 1886, p. 71.

†De Vries, Ueber die periodische Säurebildung der Fettplanzen, Vorläufige Mittheilung, Bot. Zeit., 1884.

Ueber die Periodicität im Säuregehalt der Fettplanzen, Verslagen en Mededeelingen der Koninkl. Akad. van Wetenschappen, Afd. Naturkunde, R. P. Amsterdam, 1884.

‡Ward. On some Relations between Host and Parasite. Proceedings Royal Society, Vol. 47.

||Warburg, Untersuchungen, etc., pp. 77-92.

equal, the activity of carbon assimilation increases nearly in proportion to the intensity of solar light,* or as the plants exist under more favorable conditions of light. Wollney shows that the water content† is less and the quantity of carbohydrates greater the better the plants are lighted.

One reason why shade plants when exposed to the direct light of the sun may be injured is because the form and structure of the leaves developed in the shade is different from that of plants in sunny places as shown by Stahl.‡ Groszlik§ has proved experimentally that such difference is a natural adaptation to environment.

Obstructed transpiration in conjunction with strong root pressure produces much the same condition of tissues as is found in etiolated plants. Ward says,|| "we may look on a shoot

*Wolkoff. Einige Untersuchungen über die Wirkungen des Lichtes von verschiedener Intensität auf die Ausscheidung der Gase durch Wasserpflanzen. Pringsheim's Jahrbücher, Bd, 5, S. 1-30.

Van Tieghem, Respiration des plantes submergées à la lumière d. une bougie, lieu de formation des gaz. Comptes Rendus. herbd. 1869, p. 482.

Famintzin, Die Wirkung des Intensität des Lichtes auf die Kohlensäurezerersetzung durch Pflanzen, Bulletin de l'Acad. d. St. Petersburg, Vol. 26, 1880, column 296-314.

Pringsheim, Zur Kritik der bisherigen Grundlagen der Assimilationstheorie der Pflanzen, Monatsberichte der Berliner Academie, vom Feb., 1881, S. 15 und 16, cited by Reinke, Bot. Zeitung, 1883, No. 42, 43 and 44.

Ward, Proceedings Royal Society, Vol. 47.

Sachs' Physiology.

Pfeffer Pflanzenphysiologie.

Detmer Lehrbuch der Pflanzenphysiologie.

†Wollney, Beiträge zur Frage des Einfluss des Lichtes auf die Stoff- und Form-bildung der Pflanzen. Forsch. Agr. Bd. vii, 1884. pp. 351-375, cited in Just's Bot. Jahresbericht, 1884, i, pp. 30-31.

‡Ueber den Einfluss des sonnigen oder Schattigen Standortes auf die Ausbildung der Laubblattes, Zeitschrift für Naturw. xvi, n. f. ix, 1, 2. Cited in Bot. Zeitung, 1883, s 330, and Just's Bot. Jahresbericht, 1883, ii, pp. 425-426.

§Bot. Centralb. 1884, No. 51, pp. 374-378. Just's Bot. Jahresb. 1884, i, p. 28.

||On some Relations between Host and Parasite. Proceedings Royal Society, Vol. 47, pp. 393-443.

See also Vesque et Viet. Influence du Milieu sur les végétaux, Ann. de Sci. Nat. 6th Series, Bot. Vol. 12, 1881, p. 167.

growing in a saturated atmosphere as presenting all the chief features of one growing in darkness. Its cells are extremely turgid, with watery, soft, thin walls,* and acid cell-sap; its vascular bundles feebly developed and hardly lignified; and as before it is ill adapted to withstand the exigencies of the ordinary environment."

Thus obstructed transpiration in the forcing houses through feebleness and short duration of light, and an atmosphere more humid than the average in the open during the summer months favors watery tissue, thin cell walls which are easily stretched and rapid growth in size. The weakness of the cell walls is increased through lack of sufficient building material, a result of the low degree of assimilation.

During certain processes of destructive metabolism, brought about by respiration, nitrogenous compounds like asparagin, leucin, etc., are built up. When an abundance of carbohydrates are present in the protoplasm the amides are worked up into more complex bodies. When there is a lack of carbohydrates the amides increase and the protoplasm suffers from farther decomposition.†

The simultaneous increase of the organic acids tends to overcome the tension of the protoplasm which should hold them in bounds, and they gradually diffuse through it. This may continue until the protoplasm is killed by the increase and diffusion of these substances.

This study of the environment of the plants under these conditions of forced culture and the operation of the natural forces and physiological processes leads irresistibly to the conclusion that this affection of the tomato plants is a physiological one.

Confirmed by Experiment. In order to test the effect of the

*Similar results have been obtained by students in Physiological Botany at Cornell University. Bean plants grown with lessened degrees of diffused light show corresponding grades of approach to etiolated plants and also corresponding degrees of frail, succulent tissue.

†Schulze, *Landwirtschaftliche Jahrbücher*, 1876, Bd. 5, p. 848.

Bonordin, *Bot. Zeitung*, 1878, p. 801, cited by Ward, *Proceed. Royal Soc.*, Vol. 47, pp. 343-443.

Palladin, *Ueber Eiweisszersetzung in der Pflanzen*, *Ber. d. Deutschen Bot. Gesellsch.*, 1888, p. 205.

Pfeffer, *Pflanzenphysiologie*, p. 301.

injection of excessive amounts of water into the plant the following experiment was carried out.

On Monday, December 5th, cuttings, including eight to twelve inches of the top of four tomato plants, were connected with the hydrant as follows: A cork, bored to receive glass tubing sufficient to give four delivery tubes, was inserted in a rubber hose and connected with the hydrant. The cork was then covered with resin and beeswax to prevent leakage. Small rubber tubing was then used to connect the delivery tubes with the tomato cuttings which were supported by being tied to stakes. In turning on the water it was found that the union at the cork was not water tight and it was necessary to leave the experiment until the morning of the 6th.

By this time the cuttings were badly wilted so that they drooped, and the edges of the leaves on one plant were dry. More of the resin and beeswax was brushed over the cork, melted paraffine was run over this and finally it was wrapped with a strip of cloth saturated with melted paraffine which made the union practically water tight. It was also found necessary to wire the rubber tubing to the end of the cuttings to prevent them from being thrown out by the force of the water pressure.

In turning on the water the pressure was so great it was necessary to wrap the larger rubber tube to prevent its bursting. In a few hours, the plants, though they had drooped and wilted so badly, were turgid and upright, only a few leaves of one plant which had dried at the edges not fully opening. On the 7th and 8th, during the middle of the day, transpiration being greater, the leaves were somewhat flabby though later in the day and during the night they were turgid.* By the 8th two large cushions of turgescient tissue had formed on one of the cuttings of the No. 18 variety, one on the stem about $2\frac{1}{2}$ cm long and extending about one-fourth the distance around the stem; the other one on the under side of a petiole about 3 cm long. At noon on the eighth the experiment was changed by placing a glass cage over the plants to lessen transpiration. The plants and the inside of the cage soon became so wet that water streamed slowly down.

*It was later found that iron rust accumulated slowly in the larger rubber tubes and partially clogged the vascular ducts, which accounted for the flabby condition during the middle of the day.

The cage remained on until the tenth. During this time the plants remained so wet no observations could be made on the development of the cushions.

During the preceding night the tissue of the No. 18 variety, being much more tender than the others, collapsed where the rubber tube was wired to the stem and permitted water to spurt through the delivery tube over the other plants. The cage was then removed at 8:45 A. M., and two plants were replaced with fresh ones, those being removed were the No. 18 variety and the plant the leaves of which had partially dried at the time the experiment was set up. Both of the fresh plants introduced were of the Lorillard variety. At the time of the mid-day observations on the 10th it was noted that the two other plants which had been connected four days, two days of the time under the moist cage, were drooped. They were left for another day with the hope that lessened transpiration during the night might revive them. On both of these plants, which were of the Lorillard variety, quite extended cushions were developed on the stem. On one plant were two cushions each about 3 *cm* long, on the other was one cushion 2½ *cm* long. The elevated, shining mass of cells could readily be seen so soon as they had dried after removal of the cage. December 11th these two plants were still drooped, probably not having revived during the night. They must have been near dissolution, for some of the leaves easily fell away from the stem. While there probably had been sufficient pressure on during the past 24 hours, the faucet was but a little way open and much iron rust had formed and clogged the vascular ducts at the point of union with the delivery tubes so that one of the fresh plants introduced the previous day had drooped. The three drooping plants were then replaced with fresh ones, one cutting being of the No. 18 variety and possessing quite a firm stem at the base. The water was turned on full pressure.† It was so great that within five minutes the fresh plants had been injected and water stood out in great drops at the ends of the veinlets on the edges of the leaves. This same phenomenon was observed in all the plants when freshly connected with the delivery tubes.

The exudation of drops from the edges of leaves through artificial injection of the plants has been observed by other experi-

†The pressure of the water was about 20 to 30 lbs.

menters, the water being forced into the cut end of the stem by the weight of a column of mercury*. Sachs also has produced the same effect in plants, by simply warming their roots, thus increasing root pressure.†

Some of the lower leaves had been cut from each of the last three plants connected with the tubes and from the cut surfaces a steady stream of water flowed slowly down the stem.

December 12th at 12:15 P. M., three of the plants were turgid while one was a little drooped. The epidermis of the stem and petioles of this one presented numerous longitudinal slits which perhaps offered opportunity for freer evaporation, and during mid-day when the air was comparatively dry and warm it became limp, while toward evening (4:30 P. M.) it became turgid. In one of the turgid plants several of the leaves presented quite extensive areas where the intercellular spaces were injected so that these portions of the leaf exhibited a water-soaked appearance, and drops of water stood out upon the lower surface of such areas. In all of the plants a small amount was expelled from the axils of some of the leaves, collecting in drops which flowed away at intervals.

One of the delivery tubes broke during the night of December 12th, and on the morning of the 13th the water pressure was turned off. The tube was repaired at 9 A. M. The temperature was quite low in the house during the night of the 12th, owing to an accident in the boiler room. Probably for this reason, coupled with the fact that the plants were partly covered, little transpiration took place and the plants were quite turgid. On December 14th there were no points of interest to note.

During the night of December 14th one of the delivery tubes broke again and at the time on the morning of the 15th the pressure being off, the plants had all drooped. It was not deemed necessary to carry the experiment farther, but in order to photograph the experiment fresh plants were introduced and the photo-

* Moll, J. W. Ueber Tropfenausscheidung bei Blättern. Bot. Zeit., 1880, p. 49. Moll, J. W. Untersuchungen über Tropfenausscheidung und Injection bei Blättern, Verslagen en Mededeelingen d. k. Acad. van Wetenschappen, 2, R, xv. Deel. Amsterdam, 1880. See Just's Bot. Jahrb., 1880, i, p. 239. See also Bot. Zeitung, 1880, p. 49.

† Sach's Physiology, p. 278.

graph was taken ten minutes after the pressure had been turned on. The photograph is reproduced in Plate II to show the plan of the experiment and also the numerous drops which exuded from the leaves of the injected plants, and which can be seen running down on some of the stems.

The experience had during the trial has suggested that, should it ever be repeated, it would be well to place a filter in the large rubber hose in order to remove all particles of sediment, since considerable interference arises from the clogging of the vascular ducts of the cuttings.

It demonstrates, however, the relation which excessive root pressure* bears to the development of the cushions. Their

*It matters little for the present discussion of excessive turgidity whether "root-pressure" or the laws governing the lifting of water in the stems of plants is the real cause of the elevation of the water in the tomato plants beyond the point of root absorption. It is well known that root pressure cannot lift water to the height attained by some plants and that the transpiration current is not the only factor concerned, for it goes on sometimes independently of transpiration. See the following literature :

Jamin, Comptes Rendus, 1860, 1, pp. 172, 311, 385.

Unger, Sitzungsab. d. Akad. d. Wiss. z. Wien, lvii, 1, 1868.

Sachs, Vorlesungen über Pflanzenphysiologie. Ueber die Porosität des Holzes, cited by Ward. Timber and some of its diseases, 1889.

Boehm, De la cause du mouvement de l'eau Ann. d. Sci. Nat. 6th ser., T, xii, 1881.

Elfving, Ueber die Wasserleitung im Holz. Bot. Zeit. 1882, Oct.

Hartig, Ueber die Vertheilung der organischen Substanz, des Wassers und Luftraumes in den Bäumen. Unters. a. d. Forst. Bot. Inst. München, 1882. Ueber die Ursache der Wasserbewegung in Transpirirenden Pflanzen. Ibid, 1883.

Dufour, Ueber den Transpirationsstrom in Holz-pflanzen, Arb. d. Bot. Inst. Würzburg, 1883.

Hartig, Die Gasdrucktheorie und die Sachs' che Imbibitionstheorie, Berlin, 1883. Cited by Ward, 1. c.

Zimmerman, Zur kritik der Böhm-Hartigschen Theorie der Wasserbewegung in der Pflanze, Ber. d. Deutsch. Bot. Gessellsch. Bd. i, p. 183. Ueber die Jamin'sche Kette, Ibid. p. 384.

Westermaier, Zur Kenntniss der osmotischen Leistungen des lebenden Parenchym's. Ber. d. Deut. Bot. Gessellsch. Bd. i, 1883, p. 371.

Elfving, Ueber den Transpirationsstrom in den Pflanzen, Acta Societatis Scientiarum Fennicæ, T, xiv, 1884, cited by Ward, 1. c.

Scheit, Die Wasserbewegung im Holze, Bot. Zeit, 1884, p. 177.

Godlewski, Zur Theorie der Wasserbewegung in den Pflanzen, Pringsheims Jahrb. für wissensch. Bot. Bd. xv. Heft 4, 1884, p. 569.

appearance on the stem of the No. 18 variety through the agency of artificial pressure may not seem so convincing perhaps, since this variety was very susceptible to the trouble, and it was quite difficult to obtain a cutting for the experiment which was free from it.

Their appearance on the stems of the Lorillard variety, the stems of which are much more resistant to the trouble, is quite convincing that the lack of a proper equilibrium between root pressure and transpiration is an important factor in the cause.

To be certain that the anatomical characters of the cushions developed artificially comported with those developed under the prevailing conditions in the forcing house, portions of the stems of the No. 18 and Lorillard varieties used in the experiment, on which the cushions appeared, were hardened, sectioned and prepared for study by the same method used in the preparation of the former material. The plants having been kept under the moist cage so long, their surfaces were very wet and the superficial portions of the cushions were broken down.

Plate VII represents four sections from the preparations. The two upper figures, 13 and 14, are from the stem of the No. 18 variety, while the two lower figures, 15 and 16, are from the stem of a Lorillard. Each one of the figures includes the same depth structurally of the stem, the portion represented including the epidermis, layer of chlorophyll bearing cells, the collenchyma and cortical parenchyma. In each of the varieties the left hand figure in the Plate shows the anatomical structure of the cushion, while the right hand figure shows that of the opposite side of the stem where the tissue possesses its normal form, the drawing both of the left and right hand figures being made from

Kohl, Zur Wasserleitungsfrage, Bot. Zeit, 1885, p. 522.

Errera, Eun Transpiration Versuch. Ber. d. Deut. Bot. Gessellsch., 1886, p. 16.

Zimmerman, Zur Godlewskischen Theorie der Wasserbewegung in der Pflanzen Ber. d. Deut. Gessellsch, 1885, p. 290.

Hansen, Ein Beitrag zur Kenntniss des Transpirationsstromes, Arb. d. Bot. Inst. Würzburg, 1885, p. 305.

Scheit, Die Wasserbewegung im Holze. Jenaische Zeitschrift für Naturk, 1885. Cited by Ward, l. c.

Schwendener, Untersuchungen über das Saftsteigen, Sitzungsab. d. k. preuss. Akad. Wies, 1886. See Ward.

the same section. In both varieties the epidermis, the layer of chlorophyll bearing cells, and two layers of the cells of the collenchyma participate in the radial elongation. The remainder of the collenchyma and the cortical parenchyma shows a very turgid condition as compared with the same tissue on the opposite side of the stem as shown in the right hand figure. The structural features of these artificially induced cushions do not differ from those induced under the operation of the natural forces, and we are justified in concluding that this experiment forms additional cumulative evidence that the phenomenon is a result of the unequal operation of physiological processes concerned in plant growth.

Cultural experiment. In view of the large quantities of water absorbed by the roots in excess of the actual transpiration, a cultural experiment was suggested to be governed by such conditions as might be quite easily obtained in the soil of the bed where the plants grew which were most seriously affected. For this experiment twelve potted plants of the Lorillard variety were selected, because that variety seemed to be more resistant than the No. 18.

December 7th, they were placed on boards which rested on the soil of the bed at the south side of the tomato house where the plants of variety No. 18 were growing. They were allowed to remain in this condition for two days without any water, when the soil was quite dry and the leaves were limp. They were then divided into four lots of three each.

Those of lot No. 1 were removed from the pots and transplanted in the soil bed near affected plants at the east end of the bed, the soil having been stirred previously and allowed to become partially dry.

Those of lot No. 2 were allowed to remain in the pots on the boards.

Those of lot No. 3 were removed from the pots and transplanted in the soil of the bed by the side of affected plants at some distance from those of lot No. 1.

Those of lot No. 4 were transplanted to soil by the side of the walk where were other affected plants.

NOTE.—I wish to acknowledge here the generous assistance in carrying on these experiments rendered by Professor Bailey and Messrs. Corbett and Lodeman of the Horticultural Department.

Lots 1 and 2 were now given from day to day only sufficient water to keep them growing slowly, but not enough so that at any time the plants could become very turgid.

Lots 3 and 4 were supplied with sufficient water to keep the soil nearly saturated, enough so that the roots could absorb all the water possible at their highest activity, but not so much as to interfere with that activity. The plants of lots 3 and 4 were therefore kept very turgid by the large amount of water absorbed in comparison with that given off at the leaves, and in a few days the cushions of radially elongated cells began appearing on the under side of the leaf veins and mid-rib as well as on the under side of the petioles. In a few days more the curling of the leaves was perceptible, and in about ten days the leaves of nearly all the plants of these two lots were badly affected.

Those of lots 1 and 2 presented only a very few of the cushions on the leaf veins, and if the experiment had not been disturbed probably none would have appeared. During the period of about two weeks these plants were watered quite heavily twice by an attendant who had not been apprised of the nature of the experiment. Notwithstanding this, the difference in the plants resulting in the different degrees of irrigation was remarkable. The result of this experiment seems to be conclusive concerning the physiological nature of the disease.

Relation of tissue strength to the disease. An analysis of the laws of plant growth in connection with a study of the tissue strength and firmness of the tomato plants grown in the forcing house, as well as their environment, shows that the operation of these same forces which have produced this trouble has also produced a structural condition of the plant which renders it in the highest degree susceptible. One of the most striking things about the plants of the No. 18 variety is their rank growth and the succulent condition of the stems, petioles, veinlets and mesophyll of the leaves. They are remarkable for their frail and bulky nature. The young stems and petioles of a size up to 1 cm in diameter crush between the thumb and finger with very little pressure. In this variety the stems, petioles and veinlets are very subject to the disease. In the Lorillard variety the stems have been very little affected, the trouble occurring chiefly on the veinlets of the leaf. A comparison of the tissue strength of these

two varieties gives the key to their different tendencies in this respect. A stem or petiole of the Lorillard variety of the same stage of growth is in very strong contrast with those of the No. 18. Grasped between the thumb and finger there is a sense of great resistance to pressure, and when crushed the tissue appears fibrous and little watery compared with the soft, pulpy tissue of the No. 18.

A microscopic examination of young stems of the same stage of growth of these two varieties, presents the conditions upon which this difference in firmness of tissue depends. Plate VIII, figures 17 and 18, are from camera-lucida drawings of sections of stems from a No. 18 and Lorillard plant of the same stage of growth. In the Lorillard plant considerable woody tissue has already made its appearance as is shown in figure 18. The bast cells near the cortical parenchyma have also acquired their characteristic features. In the No. 18 plant, figure 17, at the same stage of growth there are as yet no cells presenting the characteristics of woody or bast cells. The presence of the woody cells themselves probably does not exert any influence in checking the tendency on the part of the cells of the fundamental tissue to stretch under the influence of turgescence. But it indicates a slower rate of tissue growth and firmer and, therefore, more resistant cell walls in the fundamental tissue.

There is, perhaps, some inherited disposition on the part of different varieties to this trouble. The history of the No. 18 strengthens this view. The original plant was remarkable for its rank growth, abundant foliage, and wide reach of limb, so that it was trained to lateral supports similar to some methods of grape training.

But there are also individual variations in the firmness or succulent, pulpy, nature of the stems, dependent upon varying conditions of growth and environment. This is a matter of common observation in all plants. The individual variations in the succulency or firmness of the tissues of the tomato plant render them more or less susceptible to the trouble.

Relation of growth to the development of the cushions. The relation of the actively growing parts of the plant to these œdematous portions also lends support to the view that they are the result of excessive turgescence. Turgescence is one of the first conditions

of growth and, other things being equal, rapidity of growth and the proportions of the growing shoot bear a close relationship to the degree of turgescence. The greater the degree of turgescence the larger will be the cells and the thinner their walls. Where the growing shoot or leaf meets with no obstruction to growth, the multiplication of cells and their enlargement and disposition into the various tissue elements accommodates all the water which by root pressure is distributed to them. The rate of growth is sufficient to relieve the great pressure though transpiration may be below the normal rate. Transpiration takes place more rapidly in young leaves* and shoots, but I do not think the difference in the susceptibility of very young and somewhat older tissues bears any very great relation to their different capacities for transpiration as will be shown below.

In the plants which have been most susceptible to the trouble it has been very noticeable that the growing shoot for four to six inches was entirely free from the cushions, while below this rapidly growing region the turgescence effected the abnormal stretching of groups of cells. The rate of growth at this point having declined, the excessive turgescence could no longer be relieved. In making a section of a stem at this point before the radial elongation of the superficial layers of cells began, it would be possible to tell on which side of the stem, or at what points on the circumference, the cushion would be developed. All of the cells in such succulent, rapidly developed stems are proportionately large and thin walled. But the force of the excessive turgescence has produced unequal results in the size of the cells at various points in the cortical parenchyma and the adjacent collenchyma and epidermis, so that the section shows much larger cells with consequently thinner walls at one or more points outside the cambium ring.

Not only do these cells contain more water but their cell walls are less resistant. It is at these points the radial elongation of the cells takes place, as can be seen by a comparison of numerous sections of affected stems.

In farther confirmation of this fact, that active growth relieves the tension and prevents the trouble temporarily, is the following observation made on the plants of the No. 18 variety which grew

* Sachs' Physiology of plants.

on the south bench at a point where the glass was about four feet above the soil. Before the growing ends of the plants reached the glass, the terminal portion, of five or six inches, was entirely free and the plants were in all respects similar to those of the same variety grown elsewhere, though perhaps not quite so rank and succulent. When the tops reached the glass their cramped condition, the greater humidity and other contingent circumstances prevented growth or reduced it to a minimum. Turgescence, however, continued, and in a few days nearly the entire surface of the terminal portion of the plants showed the development of these cushions. The trouble extended to the very end at the base of the leaf bud, and the very young and intermediate leaves were also affected, while plants of the same variety in other parts of the house, where there was still freedom for growth of the shoots and leaves, were no different from their former condition.

Similar developments in other plants. Reference has been made to probably a similar outgrowth produced on potato stems by placing rapidly growing potted potato plants under a bell jar.*

Sorauer† also describes a similar disease on *Ribes aureum*. In this case, the outer tissues being quite firm, the radial elongation frequently takes place in the deeper lying thin walled cells. In the preparation of the plants for forcing the lateral shoots are cut off. In the spring, when placed under conditions of forced culture in the plant houses, there being few buds where growth can take place and thus relieve the stem of the great amount of water absorbed by the roots; localised centers display abnormal turgescence through the radial stretching of the cell walls.

In 1879 experiments were conducted under the direction of Sorauer, in the forcing houses at Pankow near Berlin, with well rooted stems placed under conditions favoring forced growth. The results were quite positive, excellent examples of the trouble being thus produced.

*Ward, on some relations between host and parasite, etc. Proceed. Roy. Soc., Vol. 47, 1890-1891, p. 393-443.

†Wassersucht bei *Ribes aureum*, Freihoffs' Deutsche Gärtnerzeitung, Aug., 1880. See Justs Bot. Jahresb, 1880. II Abth. p. 656-657.

Sorauer, Pflanzankrankheiten, Zweite Auflage, Bd. I, p. 235-238.

Göschke, Die Wassersucht der *Ribes*, Monatsschrift d. Verein z. Beförd. d. Gartenbaues in den kgl. Preuss. Staaten, Octoberheft, 1880, s. 451. See Just's Bot. Jahresb, 1880, II Abth., p. 657.

He cites similar developments in the stems of young plum plants in water culture where the base of the stem was set too deep in the water. Also plants of *Phaseolus vulgaris* were subject to the trouble, when cultivated in wet sand if the seedling was too deep in the soil.

Masters,* at a meeting of the Royal Horticultural Society in 1878, showed leaves of potatoes, the under surface of which was marked with warts similar to those which occur on vine leaves when grown in too close and moist an atmosphere. The conditions under which the potatoes were grown were such as to produce the growths in question.

In 1889, vine leaves were exhibited at a meeting of the same society, which possessed similar warts on the under surface. The vines were grown under glass. Ward, to whom the matter was submitted, said it was due to poor ventilation of the house whereby the humid atmosphere favored abnormal turgescence which resulted in these outgrowths.†

Quabius‡ reports the trouble on pears grown out doors, which is the same as that in *Ribes aureum*.

Conclusion. Root pressure varies greatly in different plants. It would be interesting to know if there was any variation existing in the root pressure of different varieties of tomato plants grown under the same conditions, and if there was any correlation between the unit of pressure and the susceptibility of the variety to the œdema. Or, if root pressure is constant in the different varieties, does any variation exist in the power of the stem to lift the water which the roots absorb?

The study thus far made and presented in this report is in the nature of a contribution toward a solution of the at present obscure and unequal operation of the natural forces which are associated in the etiology of this most interesting phenomenon in abnormal plant development. To fully carry out this would lead the present writer too far afield at this time upon an enquiry into the operation of the laws of plant growth under artificial conditions of environment. The subject is none the less one of

*Gardener's Chronicle, 1878, I, p. 802.

†Gardener's Chronicle, 1889, I, p. 503.

‡Wassersucht bei Birnen. Jahresb. d. Schles. Centralverein's für Gärtner und Gartenfreunde zu Breslau, 1881. See Just's Bot. Jahresb, 1872, ii, p. 704.

great importance both from a scientific and economic standpoint, and deserves serious consideration. A student of cryptogamic botany, and especially one who devotes any serious attention to the relation existing between mycology and plant pathology cannot escape an enquiry into the pathological changes induced by the action of a symbiotic organism,* or whether the symbiont merely takes advantage of a low vitality or degenerate tissues introduced through unfavorable surrounding conditions, or the unequal operation of physiological laws. So much has been demanded of the writer by the present case and until the investigation had been carried to the extent presented here, it could not be said whether or not any symbiont stood in causal relation to the trouble.

To properly conduct the enquiry farther would necessitate a broad treatment of the manifold related forces. Compartments should be arranged so that the temperature of the soil and air could be controlled independently. Several such compartments should be arranged to maintain the soil at a given temperature and vary the air temperature. Several others with a given air temperature and varying soil temperature; variations also in the humidity of the air and moisture of the soil, the latter as has been shown can be treated to control the trouble. Studies with different kinds of soils would undoubtedly yield interesting and important results, for clay soil as is well known is more retentive of moisture and would less readily yield its moisture to the roots. Means for the artificial agitation and interchange of the air should be provided. The enquiry should embrace studies of nutrition and assimilation. The effect of artificial light should be studied in connection with the trouble. Although some of the earlier experiments, with the use of artificial light cast doubt† upon the question of carbon assimilation under such conditions it has

* Symbiont here is used in the broadest sense of that term, which means a common life for a greater or less period between two organisms.

† DeCandolle, *Memoires des savans étrangers de l' Institut des Sciences*, T. I, 1806, p. 333.

Physiologie végétale, 1832, T. I, p. 131.

Biot. *Froriep's Notizen* xiii, 10, 1840.

Hervé Mangon, *Production de la matière verte des feuilles sous l' influence de la lumière électrique*. *Compt. Rend, herb. d. Sci. Paris*, 1861, T. liii, p. 243.

recently been abundantly shown that carbon assimilation takes place* and in such amounts as in some cases to be a profitable use of such means of lighting.

Finally, the question of the origination of varieties, especially

*Famintzin, Die Wirkung des Kerasin—Lamp lichtetes auf *Spirogyra orthospora* Næg, Bulletin d. l' Acad. Imp. d. Sc. d. St. Petersburg, T. 10, Column 4-14, 1865, also T. 12, col. 97-108.

Prillieux, De l' influence de lumière artificielle sur la reduction de l' acide carbonique par les plantes. Compt. Rend. d. Sci. Paris, 1869, 2d Sem., pp. 408-412.

Heinrich, Versuchs-Stationen, 1871, xiii, p. 153.

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suitied to forcing-house culture should be taken up, keeping in view the desirability of the proportionate and harmonious evolution of correlated structures and functions.

GEO. F. ATKINSON.

DESCRIPTION OF PLATES.

Plate I. Photographs showing œdematous cushions on stem and leaves of tomato.

Plate II. Photograph showing detail of connection of tomato cuttings with the hydrant, and drops of water hanging from edges of leaves which were forced through the veins by the water pressure.

Plate III. Anatomical structure of œdematous cushion on leaf vein, figure 4 healthy part of vein, figure 5 from center of cushion

Plate IV. Anatomical structure of œdematous cushion in mesophyll of leaf, near termination of leaf vein. Figure 6, appearance of small cushion magnified with pocket lens. Figure 7, section through edge of small mesophyll cushion. Figure 8, section through center of partially collapsed mesophyll cushion. Plate IV was made from specimens sent by L. R. Jones, of Burlington, Vermont.

Plate V. Structure of young œdematous cushion in young stem of No. 18 variety, showing also detail of tissue. In this and all the plates which follow, *med.* = portion of parenchyma from the pith or medulla; *w* = woody cells; *ca* = cambium zone; *b* = bast; *c p.* = cortical parenchyma; *co* = collenchyma; *ch* = chlorophyll layer of cells; *ep* = epidermis.

Plate VI. Figure 11, from center of young œdematous cushion in young stem of No. 18 variety, taken from same series as figures 9 and 10 of Plate V. Figure 12, from center of older cushion on older part of stem of No. 18 variety.

Plate VII. Comparative study of œdematous cushions produced artificially, with the normal tissue on opposite side of stem. Figures 13 and 14, from No. 18 variety; figures 15 and 16, from Lorillard variety.

Plate VIII. Comparative study of tissue firmness of No. 18 variety (figure 17) with Lorillard variety (figure 18) at same stage of growth.

SUMMARY FOR PRACTICAL PURPOSES.

The œdema of the tomato is a swelling of certain parts of the plant brought about by an excess of water which stretches the cell walls, making them very thin and the cells very large. The excess of water may be so great that the cell walls break down, and that part of the plant dying, exerts an injurious influence in adjacent parts.

The excess of water in the tissues is favored by the following conditions :

1. *Insufficient light.* The long nights of the early winter months, numerous cloudy days, and in part, the walls and framing of the forcing house deprive the plants of needed light. By a process known as *transpiration*, plants are relieved of much water when well lighted, but in poor light, since the roots are absorbing water, it is apt to accumulate to excess. Well lighted parts of the house then should be selected for the tomatoes.

2. *Too much water in the soil.* Water in excess can be withheld from the soil and prevent the trouble, and yet provide enough for the plants to grow.

3. *The temperature of the soil may be too near that of the air.* A high temperature of the soil makes the roots active, and if the temperature of the air is not considerably higher an excess of water is apt to accumulate in the plant. The aim would be then to have the temperature of the air considerably higher than that of the roots.

Lack of proper light also brings about the following harmful conditions :

1. *Acids in the plant accumulate in the dark and in strong light they decrease.* When there is an abundance of water in the plant these acids draw large quantities into the cells, causing the cells to swell, resulting many times in œdema, or in the killing of the protoplasm so that these parts of the plant die and become brown or black.

2. *Lack of light causes weak cell walls.* It is only when well lighted that plants are capable of making substances to build up cell walls with. Therefore, lack of light not only favors the accumulation of water, if other things are favorable, but it prevents the plants from building up strong tissues. In such cases plants

can *grow themselves to death*. Possibly artificial light might be used to advantage.

A quiet and close atmosphere also favors the accumulation of water in the plant. Good ventilation should then be secured. Some means for the artificial agitation or exchange of the air at night might probably be profitably devised.

Varieties of tomatos more subject to the œdema. Those with a tendency to a very rapid and succulent growth are more liable to the trouble. Tomatos which develop a firm woody young stem are less liable to it.

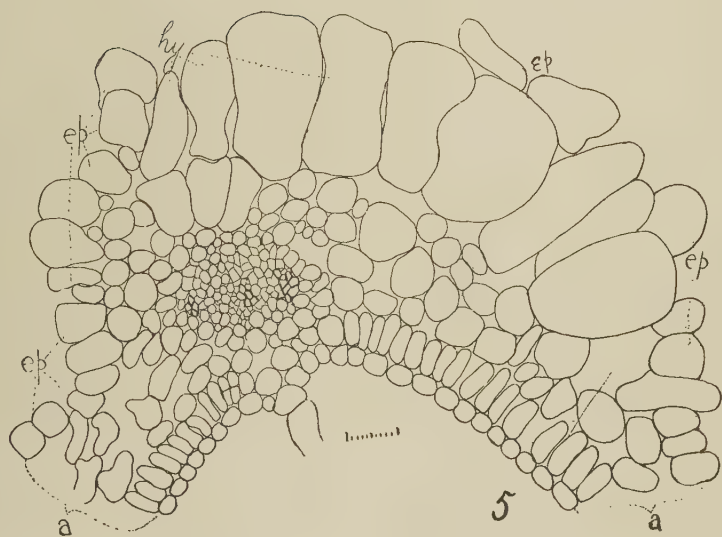
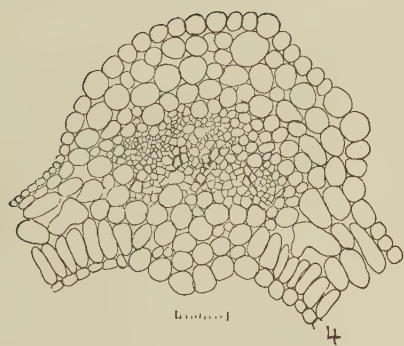
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PLATE I. *Edema of the Tomato.*

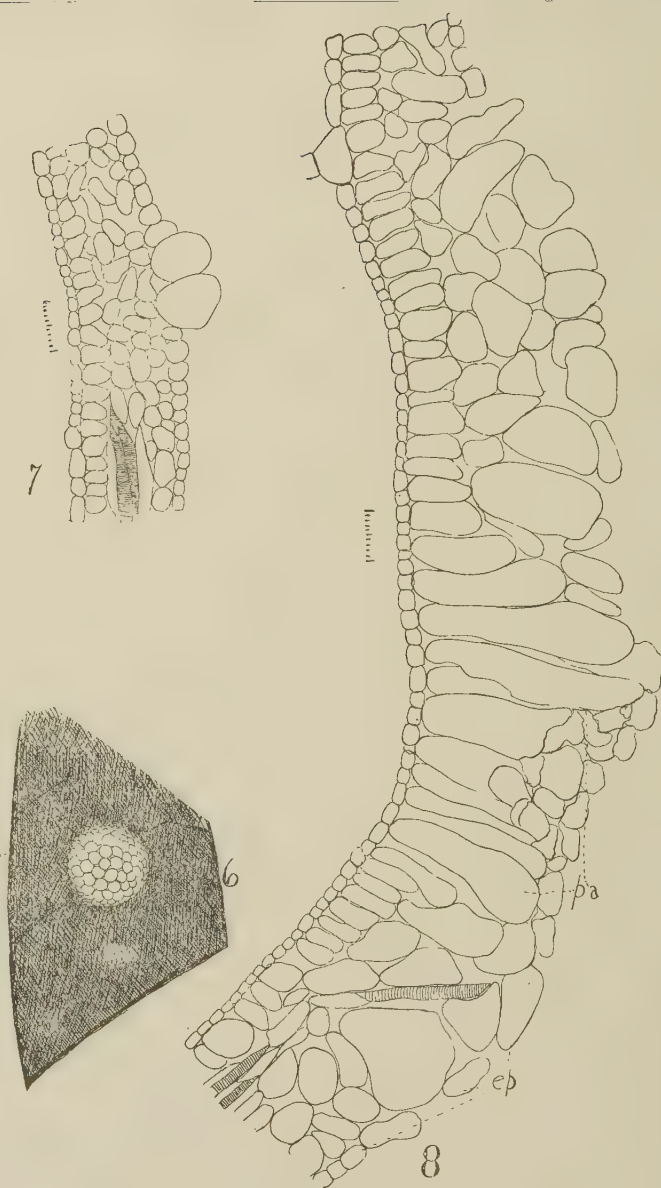


PLATE II. *Photograph of experiment for injection of cuttings with water.*



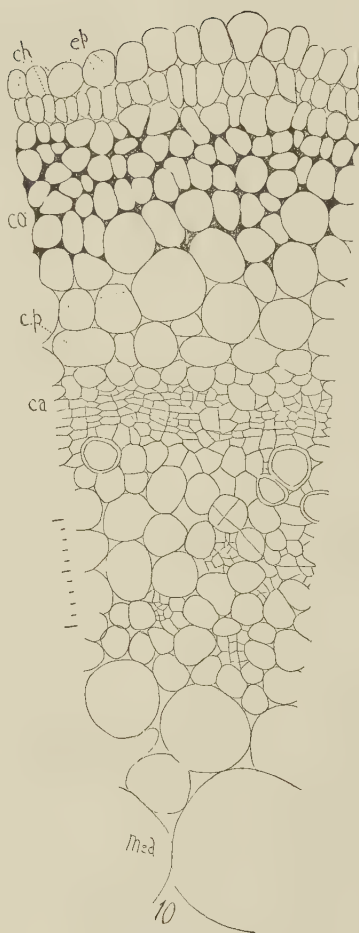
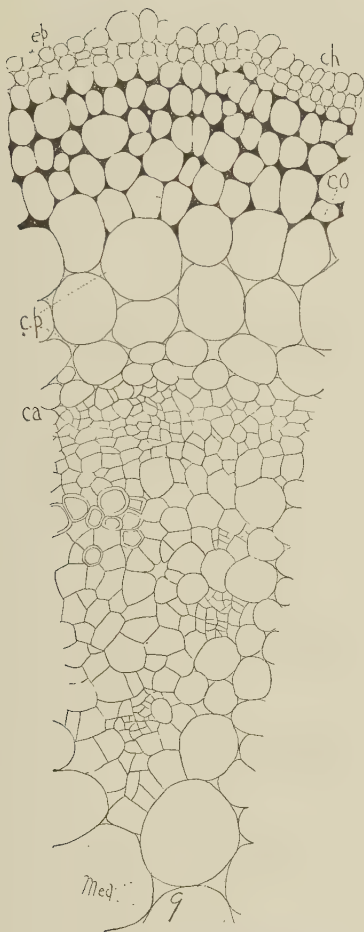
G. F. Atkinson, del.

PLATE III. *Edema of the Tomato.*



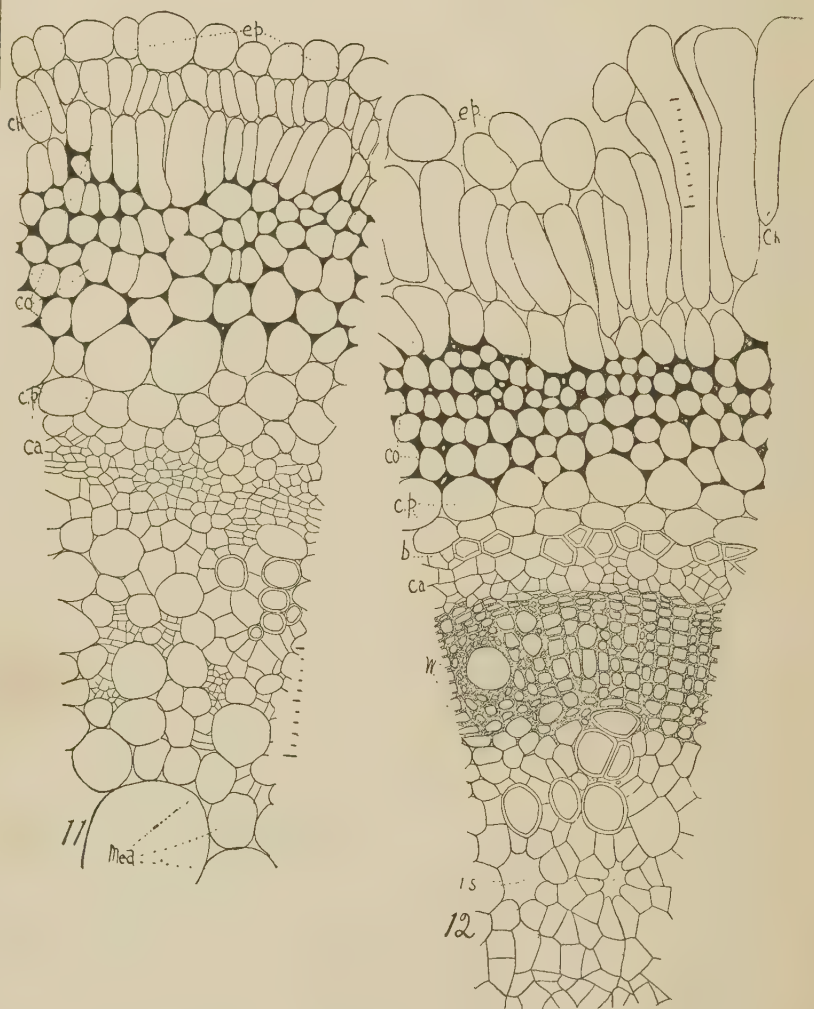
G. F. Atkinson, del.

PLATE IV. *Edema of the Tomato.*



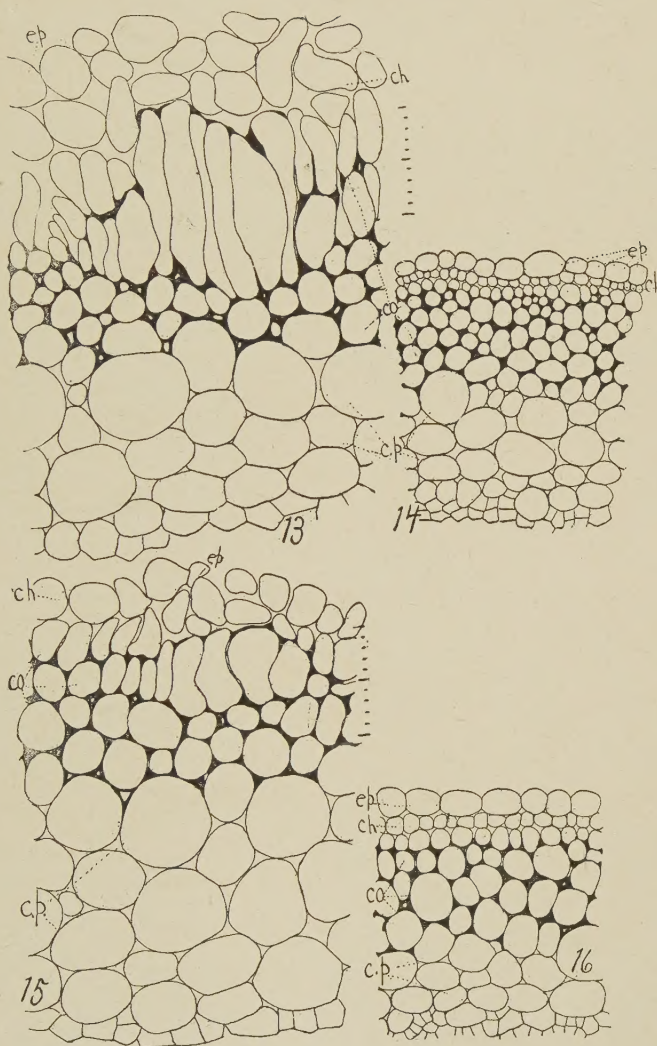
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PLATE V. *Edema of the Tomato.*



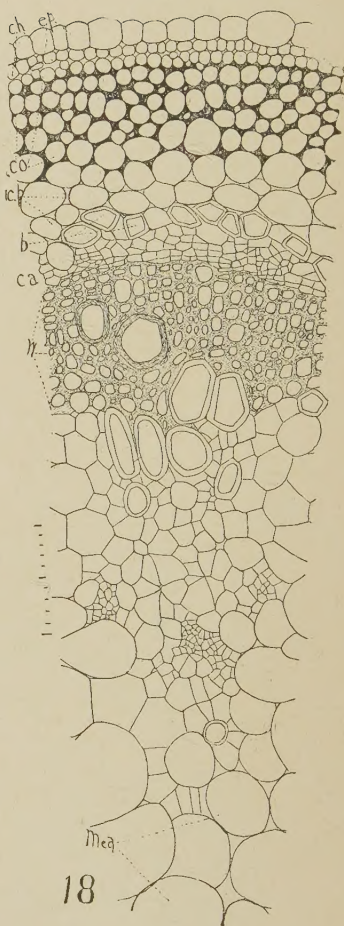
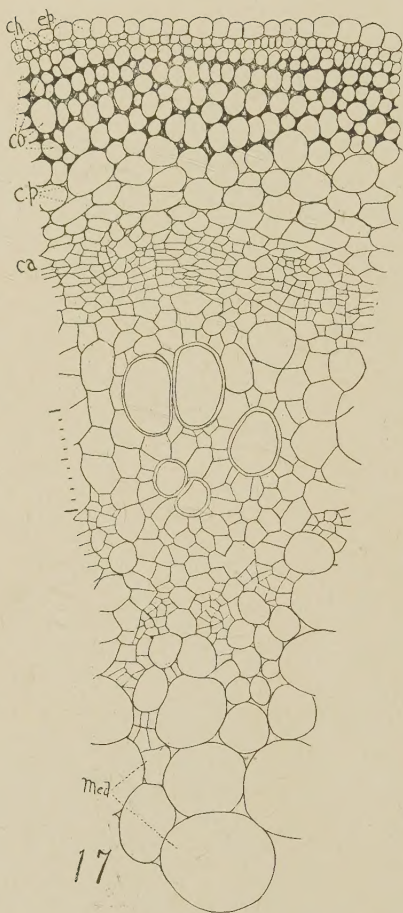
G. F. Atkinson, del.

PLATE VI. *Œdema of the Tomato.*



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PLATE VII. *Edema of the Tomato.*



G. F. Atkinson, del.

PLATE VIII. *Edema of the Tomato.*

